Seed predation in Ulex europaeus: a geographic and temporal mosaic of interactions

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Abstract

The interactions between plants and their parasites usually involve several species and present high level of variation in space and time. According to the geographic mosaic theory of coevolution, this may lead to population differentiation, large polymorphism and local maladaptation. Here we explore whether the temporal and spatial variation of the interaction between gorse (*Ulex europaeus*) and its seed predators can explain the polymorphism observed within and among populations of its native range. Indeed, gorse individuals present a polymorphism of flowering and fruiting phenology, and large variability for their susceptibility to seed predation. We performed a regular monitoring of five populations localised in Brittany (France) over five consecutive years. We observed the flowering and fruiting phenology of the gorses, and measured pods infestation rates by their two main seed predators, the weevil *Exapion ulicis* and the moth *Cydia succedana*. Flowering phenotypes and between year evolution of parasitism rates were conserved from year to year. Parasitism rates by weevils and moths increased over the fruiting period, and were negatively correlated one to another. Long flowering plants were more attacked by weevils, while short-flowering plants were more attacked by moths. However, the majority of the weevil larvae did not develop into adults, either because they were still at an immature stage at pod maturity, or because they were attacked by a parasitoid wasp. Year-to-year variations in the infestation rates by the two seed predators were very high, and depended on the population but not on the microclimatic conditions. These variations can thus explain the maintenance of the within populations polymorphism of gorse phenology and susceptibility to seed predation.

Key words: Ulex europaeus; seed predation; flowering phenology; coevolution, geographic mosaic

Introduction

Biotic interactions are a major source of specific diversity, notably in plants (Harper 1984, Thompson 1994, 2005, Burslem et al. 2005). These interactions also play a role in the intra-specific diversity of plants, particularly in regard to interactions between plants and their parasites. The main mechanisms invoked and modelled to allow the maintenance of a polymorphism of life history traits of plants as affected by parasitic pressures are negative frequency dependence (e.g. Barett 1988), trade-offs (e.g. Stearns 1992, Bonsall et al. 2002), antagonistic selection pressures (e.g. Hochberg and van Baalen 1998), and spatial or temporal variation of selection pressures (e.g. Gandon et al. 1996, Frank 1997, Nuismer et al. 2003).

To understand the ecological and evolutionary consequences of plant/parasite interactions involves taking account of several organisms. Plant pests can have competitors, predators and parasitoids (e.g. Satake et al. 2004). On the other hand, mutualists of the host plant (pollinators, seed dispersers) may exercise selection pressures which are antagonistic to those exercised by their parasites (e.g. Aizen 2003). The nature and the strength of the interactions between these participants vary in time and space, which limits their capacity for adaptation (Lively 1999, Nuismer and Thompson 2006). The multiplicity of organisms and the diversity of the mechanisms involved in the plant-parasite interactions fit in well with the geographic theory of coevolution (Thompson 1994 2005). This theory assumes that the nature and intensity of selection that the interacting species exercise on one another vary according to the population. It predicts that these spatio-temporal variations prevent the fixation of traits linked with coevolution, and leads to local maladaptations (Lively 1999, Thompson 2005).

The study of the interaction between the pre-dispersal seed predators of a plant and its phenology of flowering and fruiting lends itself particularly well to the exploration of this theory. In fact the typical seed predator develops in the fruit, and its survival depends closely on the synchronisation of its life cycle and the fruiting phenology of the host plant. Yet this phenology is determined by environmental factors which vary in time and space, and genetic factors which can evolve, notably under the effect of biotic interactions (Brody 1997, Elzinga et al. 2007).

A study of spatio-temporal variations of the phenology and the predation of the seeds can more easily be envisaged if the number of participants to take into account is limited, and if the host plant's phenology is polymorphic. This is the case with gorse, *Ulex europaeus* L. (Fabaceae). Its pods are attacked by a main seed predator, the weevil *Exapion ulicis*, which has a competitor, the moth *Cydia succedana*, and a parasite, the parasitoid wasp *Pteromalus sequester* (Barat et al. 2007). The interaction between the plant and the weevil has been studied in the context of the biological control of *U. europaeus* (Hill et al. 1991, Norambuena and Piper 2000). In fact, *U. europaeus*, which is native to Europe, has become an invasive weed in most of the countries where it has been introduced (Lowe et al. 2000). These studies have shown that the weevil only attacks pods from the spring flowering, whereas numerous plants also flower in the autumn (Hill et al. 1991). The most recent studies carried out by our team in Brittany (France) have confirmed the specialisation of the weevils on spring pods, and have demonstrated the existence of a genetic polymorphism of flowering periods, with two main phenotypes. Plants which flower only in spring, and whose pods are heavily attacked by the seed predators, coexist with plants which flower from autumn to spring, and whose pods partially escape seed predation (Tarayre et al. 2007). The maintenance of such variability within a population necessitates substantial spatial and temporal variation in predation rates. The variability between populations has been demonstrated in the previous articles (Tarayre et al. 2007, Bowman et al., in press; Atlan et al., in review).

The present paper explores the year-to-year variability of the interaction between the gorse and its seed predators to test the predictions of the geographic mosaic of coevolution. The main questions were: are the flowering phenotype and their sensitivity to seed predation

stable over years ? Are there interactions between years and populations? Do the different seed predators interfere? Is there any evidence of maladaption resulting from spatio-temporal variability? To answer these questions, we have carried out a regular monitoring of five populations localised in Brittany (France) over five consecutive years. We have studied (i) the seasonal evolution of the phenology of the gorses, of the predation of the seeds by the weevil and the moth, and of the parasitism of the weevil by the wasp, (ii) the year-to year variations of the phenology and of the parasitism rates in the different populations. The results indicate large spatial and temporal variation in success of two flowering phenotypes of gorse and of two species of seed predators. They agree with the predictions made by Thompson (2005) in the context of the geographic mosaic of coevolution.

Materials and Methods

The biological models

Ulex europaeus (Fabaceae, Genisteae) is a perennial thorny shrub widespread along the Atlantic and the Channel coasts, from Portugal to the British Isles, and is very abundant in Brittany (West of France). Most plants are about 1.5-2 m high. Its lifespan is about 20 to 30 years. The species is hermaphrodite, and pollinated by bees or bumblebees, ensuring successful pollination even during the winter months. The peak of flowering is in March, but gorse plants exhibit a high polymorphism of flowering patterns with two main phenotypes: long flowering plants bloom from autumn to spring and produce few flowers at a time: short flowering plants only bloom in spring but produce numerous flowers at a time (Tarayre et al. 2007). In Brittany, pods are infested by three types of insect (Barat et al. 2007):
- The weevil *Exapion ulicis* (Curculionidae). This weevil is a seed predator specific to gorses and used for biological control (Davies 1928, Hill et al. 1991). Females bore a hole in the pod wall with their rostrum before laying eggs inside the pod. Once hatched, the larvae burrow into the seeds and feed on them. The adult weevils are released together with the seeds when the ripe pods open.
- The hymenopteran *Pteromalus sequester* (Pteromalidae), a parasitoid wasp that develops on the larvae of *Exapion ulicis* and is released at the same time.
- Larvae of the moth *Cydia succedana* (Tortricidae). These larvae develop within pods and are able to bore a hole to leave it before pod opening. Even after the larvae have left the pods, their past presence is typically indicated by a hole and excrements.

Population monitored

Five populations were chosen in September 2000. These populations were included in the larger sample taken to compare short and long flowering plants in Tarayre et al. (2007). The same symbols were used, except for the population PG of this paper that includes the subpopulation IL of the previous paper. The distance between populations varied between 6 and 75 Km (Appendice A). Populations LO, LR and CV were inland populations located around the city of Rennes, where mean monthly temperature is at a maximum in July (18.8°C) and a minimum in January (5.4°C), and mean annual precipitation is 649 mm. Populations PM and PG were coastal populations located around the city of St Malo (70km from Rennes) where the climate is slightly more oceanic: mean monthly temperature is 17.2°C in July and 6.2 in January, and mean annual precipitation is 742 mm (data Météo France). The proportion of early flowering plants were estimated on 100 plants – when available- or from the whole set of plants in December 2000 and December 2003. The two estimations were similar and are provided in Table 1.

Table 1: Characteristics of the 5 populations of *Ulex europaeus* monitored from 2000 to 2005.

Population (Symbol)	number of individuals	percentage of long flowering plants	Habitat
Lande d'Ouée (LO)	> 200	10	heathland
La Réauté (LR)	35	29	field hedge
Chateau de Vaux (CV)	40	42	fallow
Pointe du Grouin (PG)	>200	15	seaside
Pointe du Meinga (PM)	>500	10	seaside

In each population, we randomly chose 12 individuals in September 2000. These were monitored for five years, from September 2000 to April 2005. The reproductive season of gorse lasts from September to July, and plants were monitored every month from September to February, and every two weeks from February to July. During each visit, we estimated the flowering stage of the studied individuals, and during pod maturation, we estimated seed production and parasitism.

Individuals were regularly discarded for several reasons: natural death, cutting or use of herbicide by landowners, inaccessibility due to the growth of brambles. Altogether, 45 of the 60 individuals chosen in 2000 were still monitored in 2005. In 2003, we added new individuals to keep a sample size of 12 individuals per population. In April 2005, two populations, CV and LR, were destroyed by the landowners, which prevented the measurement of pod production. As a consequence, while the flowering stages were observed over five years, pod production was measured for only four years. For simplicity, the years will be referred to as follows: 2000/2001 is year 1, 2001/2002 is year 2, 2002/2003 is year 3, 2003/2004 is year 4, and 2004/2005 is year 5.

The measurements

Flowering and fruiting stage

At each visit, we observed the presence of buds and bud size, the presence of open and faded flowers, the presence of pods, their size and their level of maturity. The date of onset of flowering corresponded to the appearance of the first open flowers, associated with the presence of many large flower buds (>5 mm), ready to open. The date of onset of fruiting corresponded to the appearance of the first mature pods, associated with the presence of many browning pods.

Pod content

At each visit we opened ripe pods to observe their contents. When enough ripe pods were available, 30 of them were opened. The proportion of pods infested by weevils was estimated by dividing the numbers of pods containing at least one weevil by the total number of open pods. The proportion of pods infested by moths was estimated by dividing the number of pods containing at least one moth by the total number of open pods. In each pod, we counted the number of seeds and the number of insects. The mean number of seeds per uninfested pod was estimated from ten pods devoid of any type of parasite. Flat, rotten or chewed seeds were not taken into account. In infested pods, we counted the number of seeds, the number of weevils (larvae and adults were counted separately), the number of parasitoid wasps (larvae and adults were pooled) and the number of moth larvae.

Statistical analysis

All analysis was performed with SAS (2005). For each year, the dates of measures were counted in days since the beginning of the gorse reproductive season (i.e. September 1st). Dates of flowering onsets were tested with the repeated measure statement of proc MIXED (Littell et al. 1998), where individuals were nested within populations and crossed with year. For the number of seeds per pods and the rates of infested pods, the same repeated measure statement of proc MIXED was used, with dates nested within years. The rates of infested pods were arcsin squareroot transformed prior to statistical analysis. Correlations were tested with the proc CORR.

Results

Flowering and fruiting phenology

The date of the onset of flowering varied greatly between individual plants, from September for the earliest to May for the latest. All plants bloomed till spring, so that flowering onset and duration were highly correlated ($N = 228$, $R = -0.88$, $P < 10^{-4}$). Flowering onset appeared to be clearly bimodal (Fig. 1), with the first peak corresponding to long flowering individuals, and the second to short flowering individuals. All five populations contained individuals of each flowering type. Year effect, population effect and their interaction were all significant ($F_{4,197}=14.35$, $P<10^{-4}$; $F_{4,60}=3.06$, $P=0.02$ and $F_{16,197}=3.00$ $P<10^{-3}$ respectively). The flowering type of individuals was preserved from year to year, as shown by the strong individual correlations between years for flowering onset (Table 2). As suggested by the interaction between year and population, the strength of the correlation depended on the population, as exemplified for year 1 and year 2 in Fig. 2. Interestingly, the best correlation between the dates of first flowering was not always obtained between successive years (Table 2).

Pods were initiated shortly after flowering, but the time for pod maturation was much longer for pods initiated in autumn or winter than for pods initiated in spring, so that ripe pods were mainly produced in spring, from March to July. Fig. 3 summarizes the typical flowering and fruiting patterns obtained during the five years of observation.

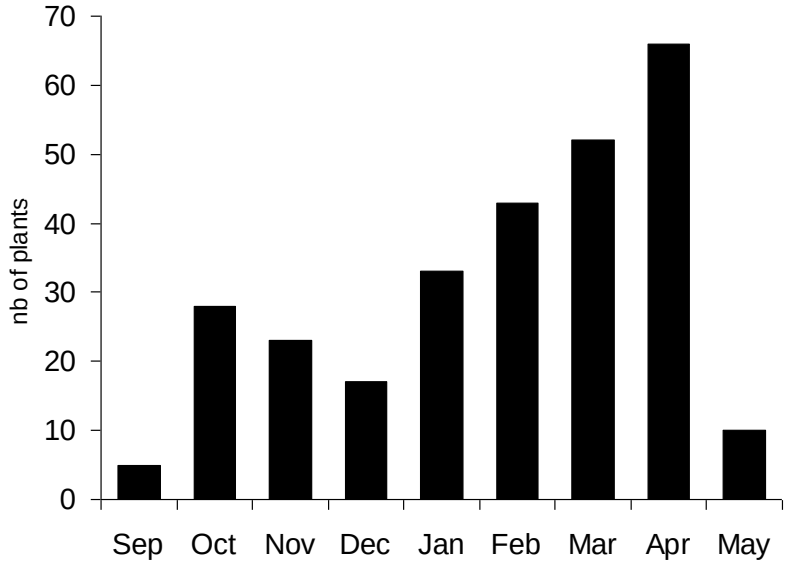

Figure 1: Distribution of the flowering onset of *Ulex europaeus* in natural populations of Brittany.

Pooled data of five populations and five years of observation (2000-2005).

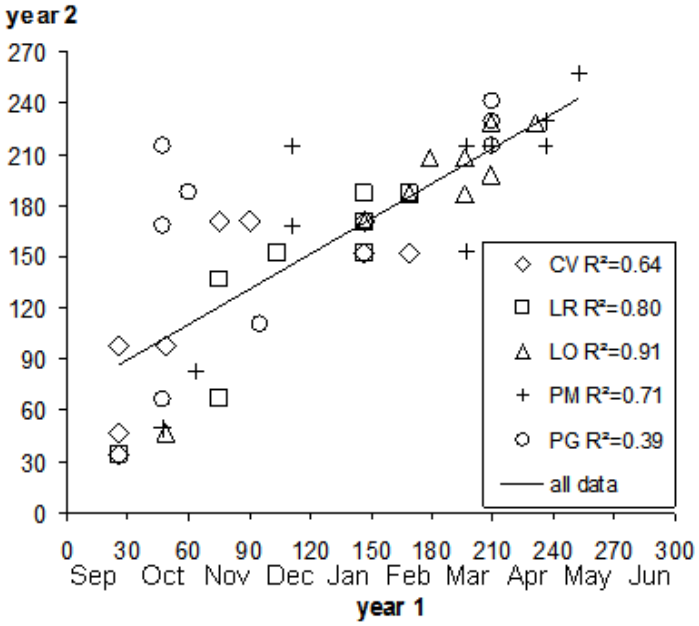

Figure 2. Correlation of the flowering onset of *Ulex europaeus* between two successive years in Brittany.
Each point represents a plant and each symbol represents a population. The linear regression is drawn for the whole set of data (see statistics in Table 2). Dates are given in day number, with September 1st as day 1, months are indicated for convenience.

Within-year variations of seed production and parasitism

The effect of the date was significant for seed production and predation (Table 3). However, while the rates of pods infested by seed predators did significantly increase with date (N=598, R=0.39, $P<10^{-3}$ for weevils and R=0.50, $P<10^{-3}$ for moths, Fig. 4), the number of seeds per uninfested pod did not show any tendency (N=515, R=0.01, P>0.1). The interactions between dates and population were all significant (Table 3), indicating that within-year variations depended on the location. However, whatever the population, weevil production began in May, while moth production began in June (Fig. 4A). Pods infested by moths always contained a single moth, but the number of weevils per pods infested by weevils varied from 2 to 14. Many weevils did not develop into adults, either because they were still at an immature stage at pod maturity, or because they were attacked by the parasitoid wasp (Fig. 4B). The reduction of seed production induced by seed predation was studied in year 3. In that year, the mean number of seeds per uninfested pods was 3.36 +/-1.56 (mean of the 5 populations +/-SD), while the number of seeds per pods infested by weevils or moths were respectively 0.64+/- 0.65, and 0.38+/-0.61.

Variation between years and populations

The year and population effect were not significant for the number of seeds per uninfested pod, but were highly significant for the rates of infested pods (Table 3). The interactions between year and population were all significant (Table 3), indicating that between year variations depended on the location. The magnitude of the between-year variations also depended on the nature of the variables (Fig. 5): large variations were observed for the rates of pods infested by weevils and moths, but small variations were observed for gorse

reproductive traits - date of first flowering and number of seeds per uninfested pod. Whatever the variable, no difference was observed between inland populations (CV, LO and LR) and coastal populations (PG and PM).

Between-year correlations of seeds per pod were positive, and more significant when consecutive years were compared. Between-year correlations of rates of infested pods were positive when significant, but the strength of the correlation were highly variable depending on the pair of years considered (Appendice B).

Seed predation of short and long flowering plants

Because seed predation increased over the reproductive season, it had to be compared at the same date for all plants. We made this comparison in the second half of June, which is the period when the largest number plants produced enough ripe pods to estimate seed predation. Short flowering plants were less attacked by weevils and more attacked by moths than long flowering plants, but the significance of these differences depended on the year (Fig. 6). The proportions of pods infested by weevils and by moths were negatively correlated ($R=-0.148$, $N=197$, $P<0.05$).

Discussion

This study has shown that the interactions of gorses and their seed predators are very variable over time and that the year-to year variations in the predation rates depend on the flowering phenotypes, on the populations, and on the species of seed predators.

Flowering types and their sensitivity to seed predation

The dates of the onset of flowering are distributed bimodally. This bimodality, already seen after one year of observation by Tarayre et al. (2007) is even more marked after compiling the results of five years of study, confirming the existence of two distinct phenotypes. The between-year correlation of the dates of the onset of flowering is strong, but interestingly, the highest values are not necessarily found between consecutive years (Table 2), suggesting that the age of the plant has little to do with these variations. The year effect must therefore be essentially plastic responses to weather variables such as temperature or sunshine, which influence the date of the start of flowering in most species (reviewed in Kelly and Levin 2000).

Whatever the flowering period, the production of seeds per pod was constant, but the rate of seed predation increased during the course of the season, confirming previous results (Tarayre et al. 2007, Barat et al. 2007). The years with a high parasitism rate thus favour long-flowering plants, which produce most of their pods before the peak of seed predation. However the relative fitness of the two flowering phenotypes depended not only on the overall rate of parasitism, but also on the nature of these parasites. In fact the long flowering plants were more attacked by weevils, while the short-flowering plants were more attacked by moths. The existence of a negative correlation between attack by the weevil and by the moth indicates either strong competition between these species, or a trade-off in between plant defence against the two species. Indeed, although it is not always the case, it is not rare to observe negative correlations between plant defences to different parasites (Koricheva et al. 2004).

Mismatch between the development of the weevils and the maturation of the pods

The majority of the weevil larvae do not have the time to develop into adults during the maturation of the pods, and only the latest pods produced more adult weevils than immature forms condemned to die. There is thus a mismatch between the time of development of the weevil and the fruiting phenology of the gorse. According to Thompson (2005), this

mismatch may result either from the temporal dynamics of the coevolution, due to "*transient mismatches within local communities, as species respond sequentially to one another*", or to its spatial dynamics "*coevolving traits are well matched in some localities and mismatched in others*". The first hypothesis suggests that the maladaptation of the weevils would result from a delay in their arms race against the gorse (Kareiva 1999). By producing early pods and/or ones that mature more rapidly than the development of the weevils, the gorse plants cause the weevils to suffer a big setback. The weevils will then be selected to accelerate their development, and one might imagine that the next step in the evolutionary process will see the weevils adapt to the maturation time of the gorse pods. From the spatial point of view, coevolution, if it has occurred, would have happen in the centre of origin of these species, the Iberian peninsular, where the mean temperatures are higher than in Brittany. Yet it is probable that the synchronisation between the development of the insects and the maturation of the pods depends on the temperature. Both are accelerated by heat and slowed down by cold, but this effect can be different for plants and for plant pests (Yukawa and Akimoto 2006). An observation of weevils coming from contrasting climatic zones might reveal geographical variations in the adaptation of weevils to the flowering of gorse. If the synchronisation of the weevils and the gorse increases with warmth, it should increase with the advancement of the season, which in fact is what is observed. One may wonder therefore why the weevils do not lay their eggs just in the latest pods. However, the number of plants producing fruits in July is low, whereas as the season progresses the weevils have to confront two enemies – a competitor, the moth, and a parasitoid, the wasp. The adjustment between all these variables appears all the more difficult when the year-to year variations are large and unpredictable.

Year-to year variations of life history traits

All the variables studied present large year-to-year variations, which differ according to the population. However, whereas the variations are only a few percent for the variables linked to the development of the gorse, (date of the start of flowering, number of seeds per pod), they can vary by a factor of 10 to 30 -fold for the variables linked to the parasitism by the weevils or the moths (Fig. 5). In fact, for the dates of the start of flowering several constants appear. For example the CV and LT populations are the earliest and the LO and PM populations are the latest, whichever year is considered. These differences do not seem to be linked to localisation inland or on seaside, and probably involve other environmental factors than microclimatic variations. On the other hand, the variations in the extent of parasitism between populations depend on years, the flowering phenotype and the type of seed predator considered. For example for the CV and LR populations, the highest rates of parasitism by weevils were observed in year 3, but the highest rates of parasitism by moths was observed in year 2. For the moths, a parasitism peak is observed in year 2 for the CV and LR populations and in year 3 for the LO and PG populations. Also, the long flowering plants are more susceptible to the weevils and the short flowering plants are more susceptible to the moth, but the magnitude of this difference depends on the year: it is not significant in year 1, only for moths in year 2, only for weevils in year 3, and very large for both seed predators in year 4 (Fig. 6). This absence of a clear trend makes local adaptation very difficult, and explains the absence of a correlation between the rate of parasitism and the proportion of long-flowering plants observed in year 2 in this same region (Tarayre et al. 2007).

Maintenance of the polymorphism

Both flowering phenology and resistance to seed predators appeared to be genetically determined and highly polymorphic in natural populations of *U. europaeus* (Tarayre et al. 2007, Atlan et al., in review). Fluctuations between years in fitness can allow polymorphism to be maintained within populations, but only in rather restricted conditions (Gillespie 1991).

Haldane and Jayakar (1963) showed that polymorphism could be stable if the variance in the reproductive success of the phenotypes differs, and if the most variable phenotype is recessive. By flowering in two seasons, the long-flowering plants produce pods devoid of seed predators, and thus decrease the variance in their reproductive success between years. In contrast, the plants that only flower in spring have a reproductive success that is directly related to the biotic and abiotic conditions of a single season, and therefore have a greater variability between years. The short flowering phenotype is thus the most variable, and it has been shown to be recessive (Atlan et al., in review), in accordance with the prediction of Haldane and Jayakar (1963). This study showed that the year-to-year variability of parasitic pressure in spring is highly variable and not predictable from the location or the particular weather conditions of a given year. The conditions for the maintenance of a polymorphism of flowering phenology by fluctuations between years are therefore met. Beside this polymorphism, we found another polymorphism for the resistance to weevils and moths in spring, although the traits involved have not yet been identified. Hedrick (2002) showed that such a polymorphism can be maintained if different alleles confer resistance to different pathogens, which is unknown, and if the pathogens differ in their proportion over time, which is clearly the case in natural populations of gorse. Thus the temporal pattern of interactions appears to be by nature sufficient to maintain the polymorphism observed within the population, while the spatial pattern of seed predation can explain the differences observed among populations.

A geographic mosaic of coevolution

This study was performed in a relatively restricted geographical area. However, even at this restricted scale, the interaction between gorse and its seed predators is in agreement with the three ecological predictions of Thompson (2005) under the assumptions of the geographic mosaic theory of coevolution: (i) populations differ in traits shaped by biotic interactions, here plant phenology and resistance to seed predation, (ii) traits of interacting species are mismatched in at least some communities, since weevil developmental time and pod maturation are not synchronized, (iii) few coevolved traits are favoured across all populations and fixed within the species, as attested by the high level of polymorphism observed within and among populations. The interaction between gorse and its seed predators is therefore a good example of polymorphisms maintained by the temporal and geographical mosaic of selection pressures.

Acknowledgements

This work was supported by a CNRS grant (ATIP). We are grateful to Louis Parize for technical assistance, and Agnès Schermann, Valérie Roussel and Luc Gigord for helpful comments. We also thank Alan Scaife for English translation.

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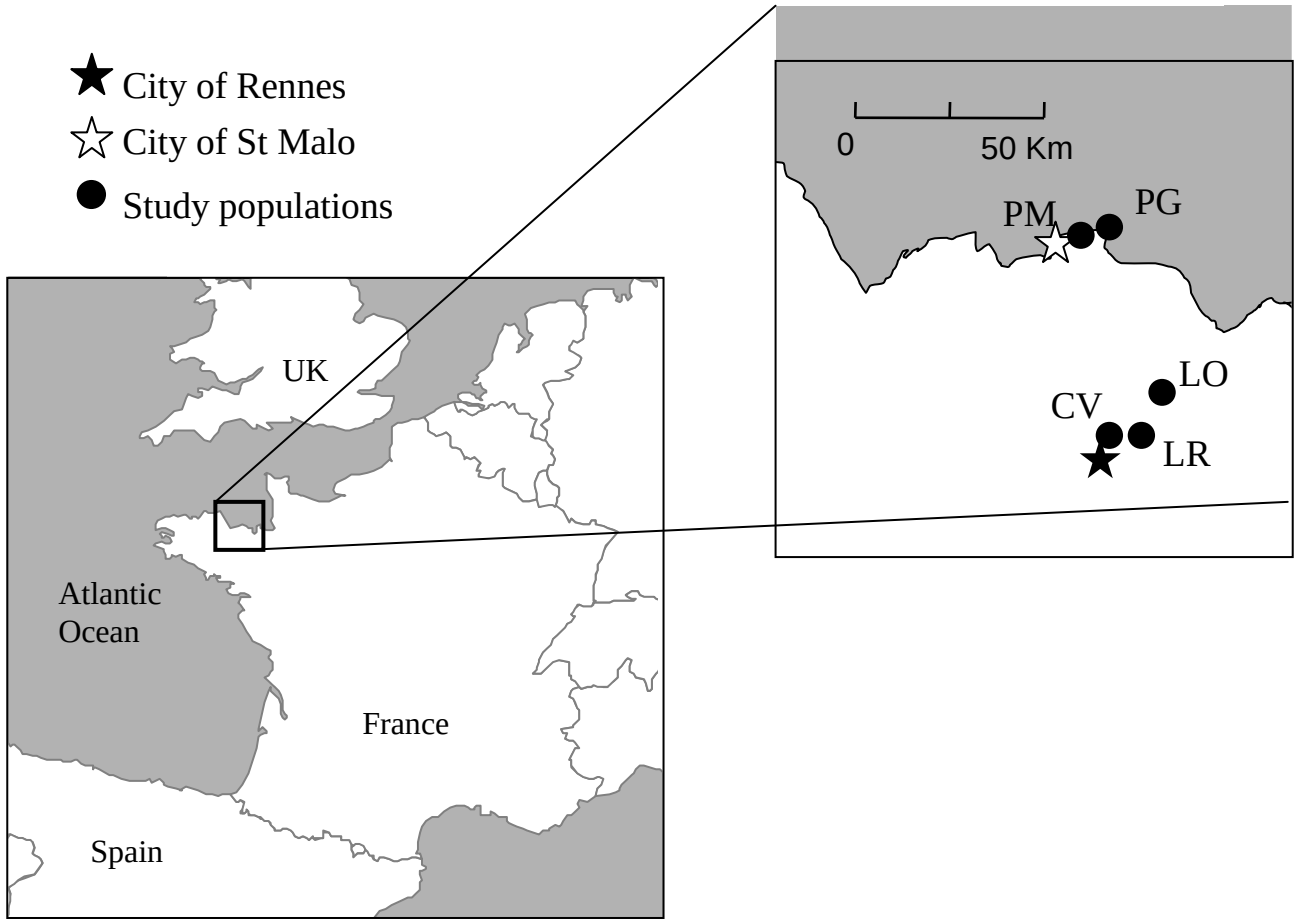

Figure A: Location of the study populations

APPENDICE B – Atlan et al.

Between years correlations of pod content in natural populations of *Ulex europaeus* in Brittany.

For each pairwise correlation, the tables gives R the Pearson coefficient, N, the sample size, and P, the probability. Data of the five populations were pooled.

	Number of seeds per uninfested pod			Proportion of pods infested by weevils			Proportion of pods infested by moths		
	Year 2	Year 3	Year 4	Year 2	Year 3	Year 4	Year 2	Year 3	Year 4
Year 1	R=0.60 (N=29) $P<10^{-4}$	R=0.38 (N=19) P=0.10	R=0.31 (N=29) P=0.11	R=0.54 (N=29) P<0.01	R=0.43 (N=22) P<0.05	R=0.51 (N=28) P<0.01	R=0.42 (N=29) P<0.05	R=0.39 (N=22) P=0.07	R=0.31 (N=28) P=0.11
Year 2		R=0.73 (N=16) P<0.01	R=0.39 (N=31) P<0.05		R=-0.19 (N=21) P=0.39	R=0.36 (N=31) P<0.05		R=0.49 (N=21) P<0.05	R=0.58 (N=31) P<0.01
Year 3			R=0.43 (N=21) P=0.05			R=0.38 (N=28) P=0.84			R=0.23 (N=28) P=0.24

Table 3: Results of ANOVA on pod production and seed predation of *Ulex europaeus* in Brittany (France).

	Seeds per uninfested pod (N=510)				% pods infested by weevils (N=593)				% pods infested by moths (N=593)			
Source	df^n	df^d	F	P	df^n	df^d	F	P	df^n	df^d	F	P
Population	4	77	1.17	NS	3	77	4.09	<0.01	3	77	21,36	$<10^{-3}$
Year	3	102	2.32	NS	4	119	25.4	$<10^{-3}$	4	119	89,74	$<10^{-3}$
Date(year)	57	231	4.98	$<10^{-3}$	60	290	8.24	$<10^{-3}$	60	290	4,23	$<10^{-3}$
Pop x year	10	102	2.29	<0,05	11	119	2.49	<0.01	11	119	25,37	$<10^{-3}$
Pop x date(year)	25	231	1.76	<0.05	28	290	2.19	<0.01	28	290	2,17	<0.05
NMLR	1	K^2=205	χ^2=205a	$<10^{-3}$	^{2}=2	1	K^2=205	χ^2=69.3a	$<10^{-3}$	^{2}=2	1	K^2=205	χ^2=17.3a	$<10^{-3}$

N=number of measures, Df^n, Df^d = degrees of freedom of numerator, denominator. NS: P>0.05, NMLR: Null Model Likelihood Ratio.

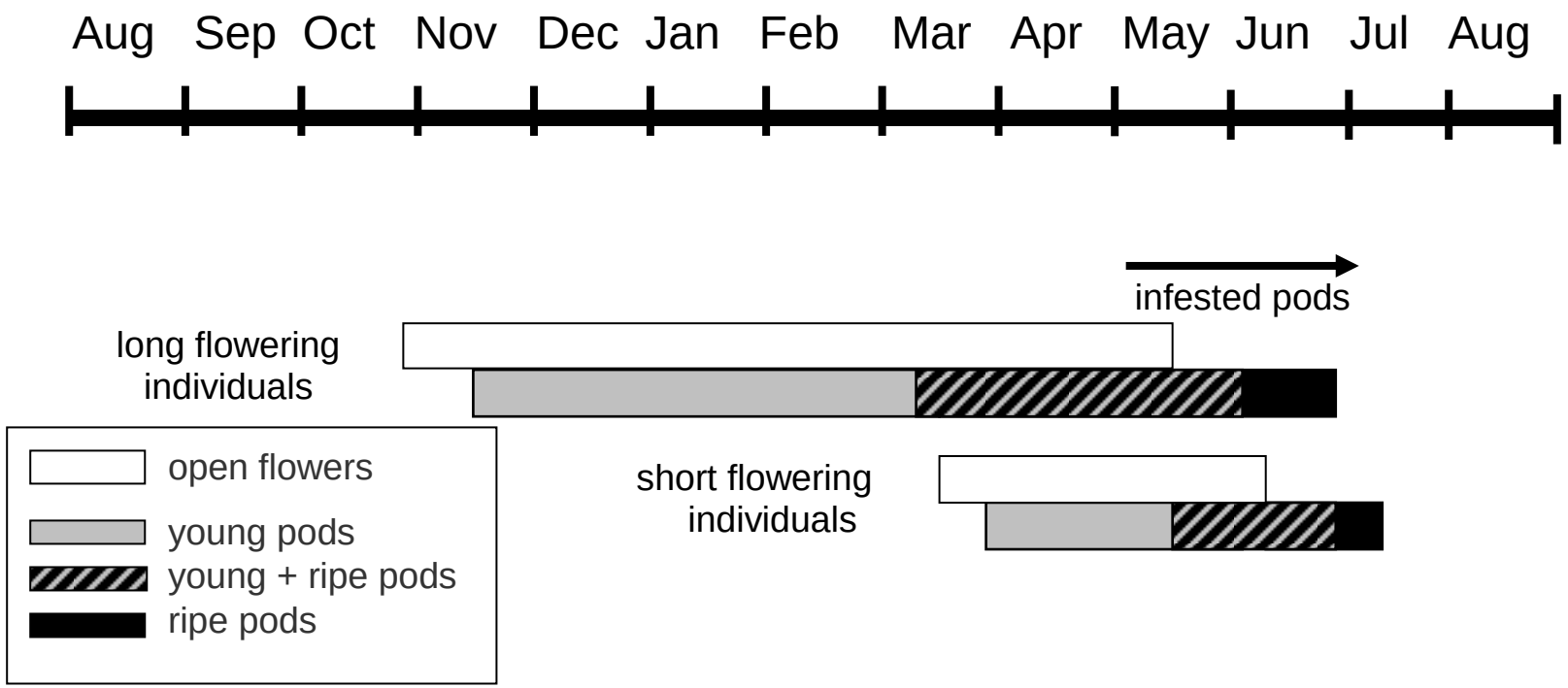

Figure 3: Flowering and fruiting phenology of Ulex europaeus in Brittany.
This figure summarizes the flowering pattern of typical long and short flowering plants (synthesis of five years of monitoring in five natural populations).

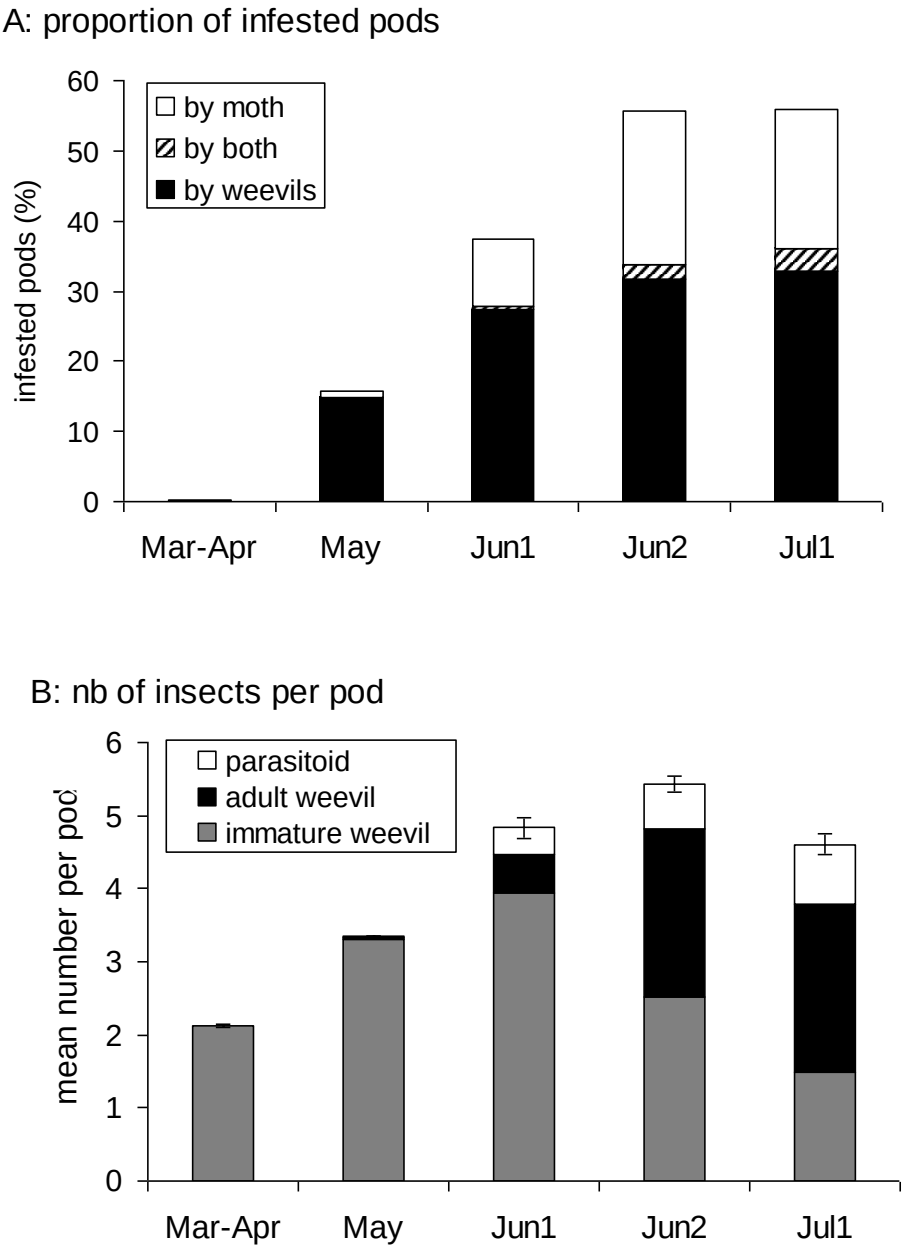

Figure 4: temporal variation of seed predation in natural populations of *Ulex europaeus* in Brittany.
A: proportion of infested pods, B: mean number of insects per pod infested by weevils. Means of the five years of observation are given +/- standard error. Five periods were considered: March-April (N=30), May (N=111), first half of June (N=148), second half of June (N=167), first half of July (N=126).

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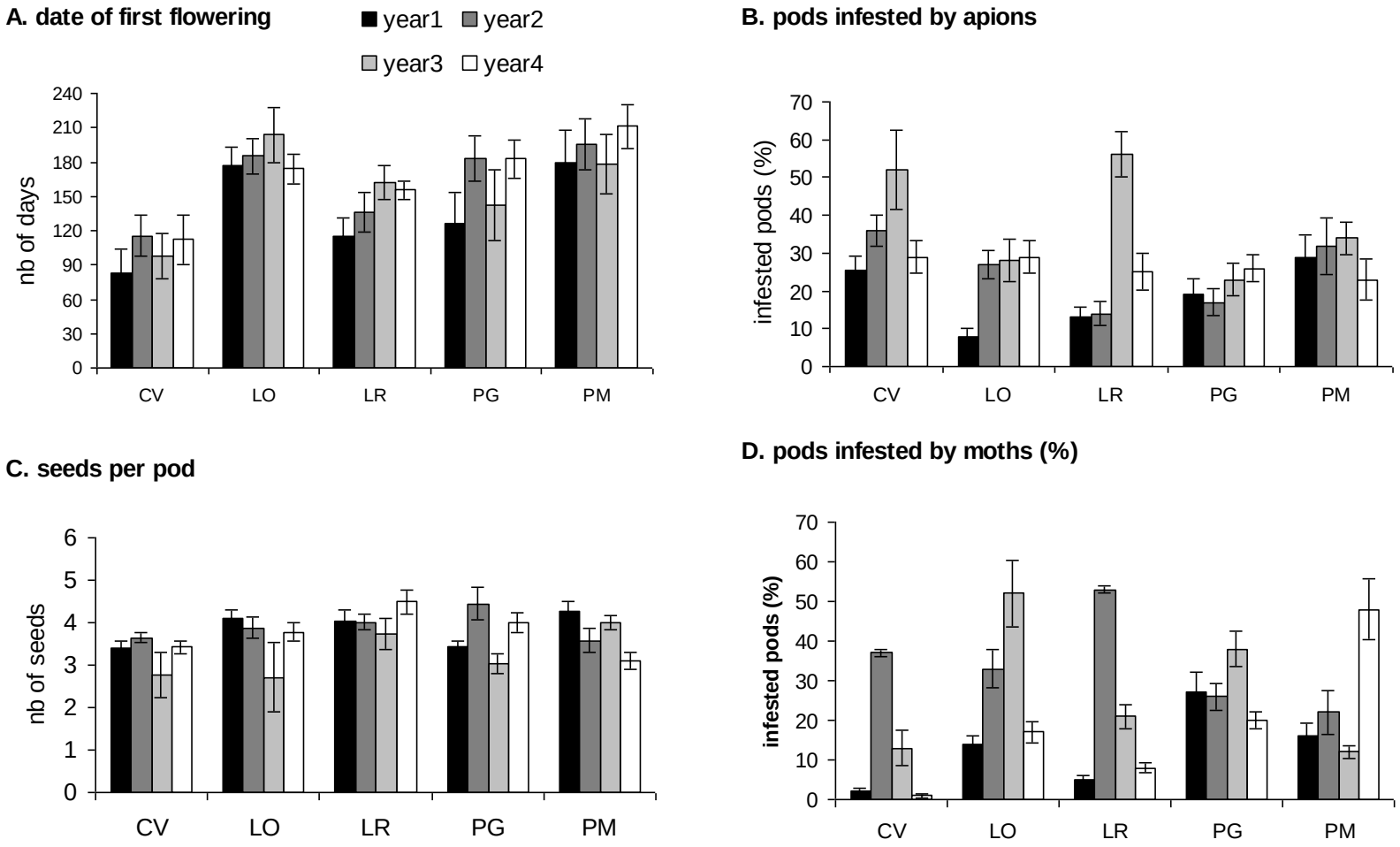

Figure 5: Variation between years and populations of reproductive traits of *Ulex europaeus* in Brittany.
This figures gives the population means for each year of the date of first flowering (A), the mean number of seeds per pod (B) and the mean rates of parasitism per weevils and Moth (fig C and D). Means are given +/- standard error.

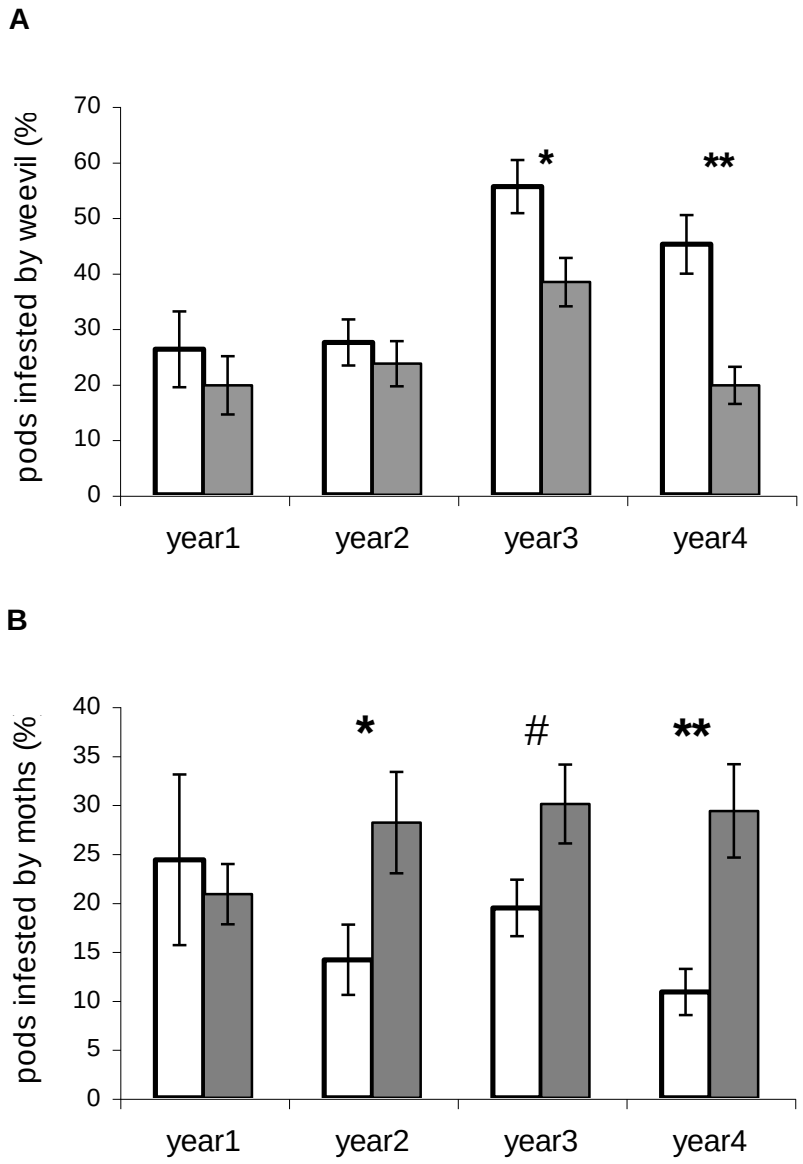

Figure 6: Comparison of the proportion of infested pods in short and long flowering plants of *Ulex europaeus*.
A. pods infested by weevils, B. pods infested by moths. White bars: long flowering plants; grey bars, short flowering plants. Data of the five populations are pooled. Differences between flowering types were tested within each year by a one-way ANOVA. N varies from 32 to 54 depending on the year.
P<10%, *P<5%, ** P<1% (one way ANOVA within each year).